Microbial Productivity and Community Growth Rate Estimates in the Tropical North Pacific Ocean

Christopher D. Winn
David M. Karl

Department of Oceanography
University of Hawaii
Honolulu, Hawaii

Abstract Microbial productivity and growth rates were estimated from rates of nucleic acid synthesis in the oligotrophic North Pacific Ocean near the Hawaiian Islands. A rate of total microbial production equivalent to 400 mg C m^{-2} day^{-1} and a growth rate of 0.4 to 0.5 doublings day^{-1} was measured in the 0–150 m depth interval. The rate of total microbial production in the 150–900 m depth interval was 790 mg C m^{-2} day^{-1}, almost twice as great as in the overlying waters. Microbial growth rates in this depth interval ranged from 1.1 to 2.4 doublings day^{-1}. ATP measurements indicated that from 10 to 30% of the POC in the photic zone is composed of living carbon, that living biomass is in approximate steady-state, at least on the scale of days, and that there are no diurnal biomass fluctuations in this environment. Measurements of ATP in incubation bottles showed that systematic fluctuations in ATP concentrations do occur during in situ incubations.

KEY WORDS: North Pacific, nucleic acid synthesis, microplankton, growth rate

Biological Oceanography, Volume 3, Number 2
0196–5581/84/010123–00$02.00/0
Copyright © 1984 Crane, Russak & Company, Inc.

HIG Contribution No.

Introduction

Substantial progress has been made in the study of microbiological oceanography in the past 20 years, especially with regard to the standing stocks of microorganisms and the rates of primary production in the sea. In general, numerous modifications of the $^{14}CO_2$ technique, originally proposed by Steeman Nielsen (1952) have been used for the measurement of primary production (see Peterson, 1980, for a detailed discussion of the use of the $^{14}CO_2$ method). The wide-scale application of this technique has provided us with what is believed to be a fairly accurate picture of global marine productivity (Koblentz-Mishke, Volkovinsky, and Kabanova, 1970). These studies have shown, for example, that the majority of primary production occurs in the oceanic realm in spite of the fact that production rates (per unit volume) may be much greater in neritic waters (Ryther, 1969). It should be pointed out, however, that the $^{14}CO_2$ technique is not universally accepted as an accurate measure of total microbial community carbon production, since the repackaging of soluble organic carbon by microheterotrophs, which may not be accounted for by this technique, can represent an important pathway for carbon and energy flow in certain environments (Pomeroy, 1974; Sieburth, 1976). Furthermore, a number of studies have indicated that the $^{14}CO_2$ technique may substantially underestimate the actual rate of primary production, especially in oligotrophic oceanic habitats (Sheldon, Prakash, and Sutcliffe, 1973; Sieburth et al., 1977; Sheldon and Sutcliffe, 1978; Tijssen, 1979; Postma and Rommets, 1979; Johnson, Burney, and Sieburth, 1981; Shulenberger and Reid, 1981; Jenkins, 1982).

At present two opposing hypotheses, based on data resulting from different experimental approaches, exist regarding the in situ growth state of oligotrophic phytoplankton communities. Using $^{14}CO_2$ incorporation and estimates of phytoplankton standing stock (Eppley et al., 1973; Sharp et al., 1980), growth rates appear to be low in the open ocean, presumably because of nutrient limitation. Alternatively, if one relies on measurements of phytoplankton elemental ratios (Goldman, McCarthy, and Peavey, 1979), growth rates appear to be near maximal because

of the rapid and efficient recycling of scarce nutrients in these environments.

During the past few years investigations in our laboratory have focused on the development and evaluation of a new experimental approach to the study of growth and metabolism of oceanic microbial communities (Karl, 1979; Karl, Winn, and Wong, 1981a, 1981b; Karl, 1981; Karl, 1982). This approach involves the measurement of the rates of synthesis of both ribonucleic acid (RNA) and deoxyribonucleic acid (DNA). Since nucleic acids are essential components of all organisms and since the rate of nucleic acid synthesis ultimately controls the growth rate of microorganisms, this technique promises to yield independent estimates of the rates of production and growth of microbial assemblages in nature.

In this report we will use the term "microbial production" to describe estimates of organic carbon production extrapolated from nucleic acid synthesis rate measurements. This measurement includes not only the production from inorganic carbon via autotrophic growth but also production from recycled organic carbon via heterotrophic growth. The term "carbon production" will be reserved for measurements of $^{14}CO_2$ primary production and refers specifically to the rate at which organic carbon is produced from inorganic carbon.

Materials and Methods

Station Location and Sampling

The research reported here was conducted on a cruise aboard the R/V *Thomas Thompson* in February 1980. The station was located approximately 100 km southwest of the island of Hawaii (Figure 1). Temperature, salinity, and density (σ_t) profiles for this station are shown in Figure 2.

Water samples were collected in acid-washed 30- and 12-l Niskin^R bottles. All samples were gravity prefiltered through 90 μm Nitex^R mesh prior to analysis. Particulate materials for determination of adenosine-5′-triphosphate (ATP) were concentrated onto Whatman^R GF/F glass fiber filters which were immediately immersed in boiling 60 mM PO_4 buffer (pH 7.4). ATP was mea-

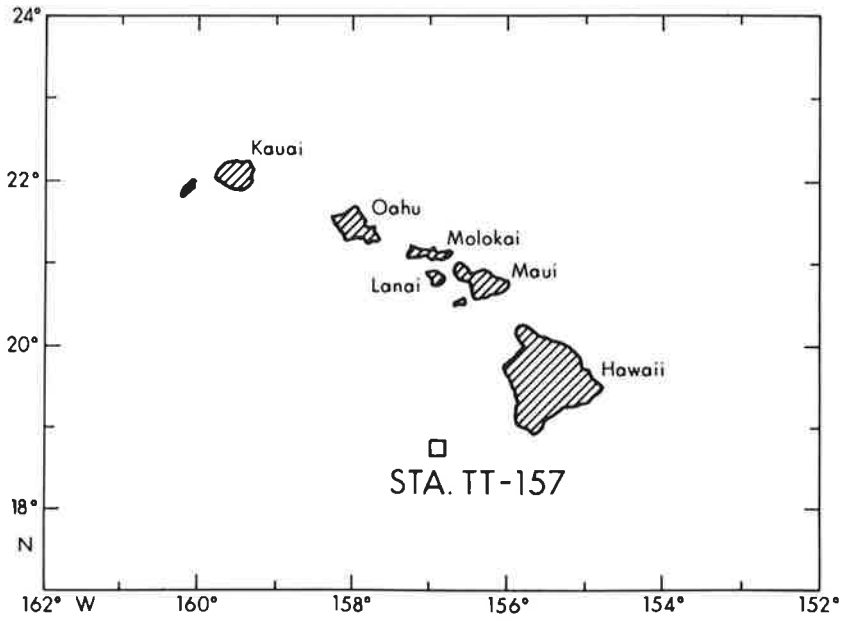


FIGURE 1. Station location (18°43.8′N, 156°50.4′W) about 100 km southwest of the island of Hawaii.

sured using the firefly bioluminescence assay procedure (Karl and Holm-Hansen, 1978). Samples for particulate organic carbon (POC) and particulate organic nitrogen (PON) were collected on combusted GF/F filters and analyzed according to the method of Sharp (1974).

Incubations

Incubations were performed using ^{3}H-adenine, both on deck and in situ in acid-washed 2-l and 500-ml polycarbonate bottles. The in situ incubations were deployed using a free-floating incubation array, for depths to 150 meters, or on the ship's hydrowire for deeper incubations (150–900 m). In situ incubations were conducted for 5 h (0–150 m) and 6.5 h (250–900 m). For shipboard incubations (0–150 m depths only) the bottles were maintained in clear Plexiglas tanks through which surface seawater (approximately 26°C) was continuously circulated. In situ light level was simulated using neutral density filters.

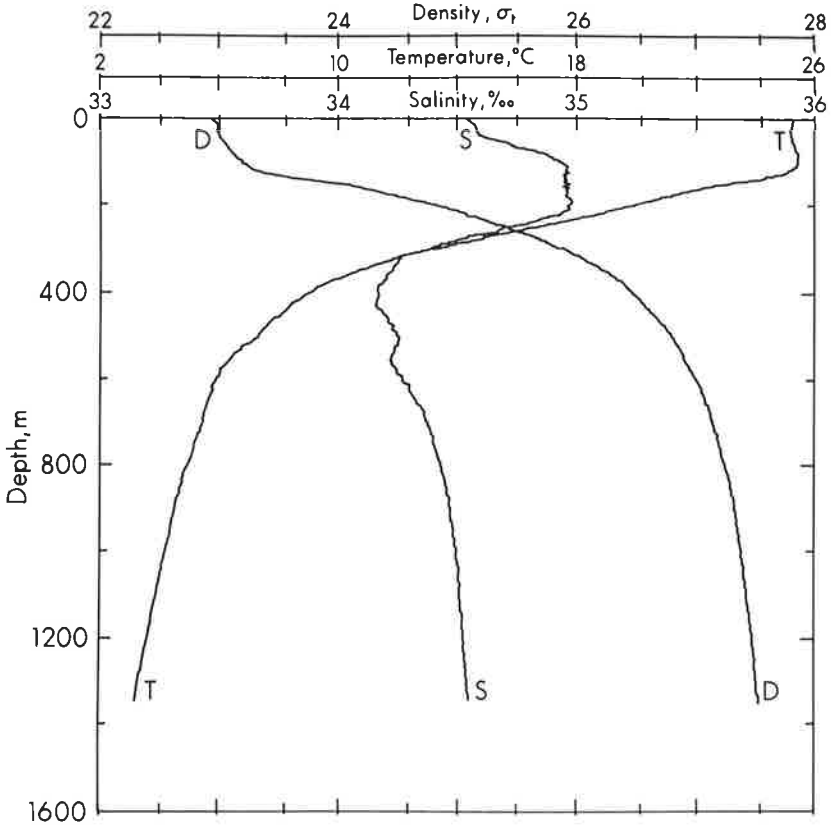


FIGURE 2. Temperature, salinity, and density (σ_t) profile at station location. Data courtesy of C. J. Lorenzen.

For the purposes of this paper the 0–150 m depth interval will be referred to as the "photic zone," since the 0.1–1.0% light level is approached at approximately 150 m in these waters (Bienfang and Gundersen, 1977). The 150–900 m depth interval will be referred to as the "intermediate depth."

Isotopes

[2-^{3}H]-adenine obtained from New England Nuclear (specific activity 20 Ci mmol^{-1}) was used for all experiments. The isotope was diluted to a working stock of 100 μCi ml^{-1} with sterile distilled water and stored frozen (−20°C) prior to use. Isotopes

were added to incubation bottles at concentrations of 100 $\mu Ci\ l^{-1}$, which was equivalent to the addition of 5 nM adenine.

Rates of Nucleic Acid Synthesis

Nucleic acid rate measurements were made according to the methods outlined previously (Karl, Winn, and Wong, 1981a; Karl, 1981). The rates of synthesis of both RNA and DNA were calculated, except where otherwise noted, by the methods of Karl, Winn, and Wong (1981a). Briefly, this technique measures the rates of both RNA and DNA synthesis via the incorporation of ^{3}H-adenine, a purine precursor to both RNA and DNA. The rate of synthesis is determined by dividing the incorporation of ^{3}H-adenine (nCi l^{-1}) into RNA and DNA by the measured specific radioactivity (nCi $pmol^{-1}$) of ATP, the intracellular precursor to adenine incorporation into nucleic acids. Rates are expressed as pmol of adenine incorporated into nucleic acid l^{-1} h^{-1}. Radioactivity was measured using a Searle (model 6890) liquid scintillation counter with Aquasol II (New England Nuclear) as the fluor. Channels ratio was used to measure and correct for quench.

Results

POC and ATP Concentrations

Measurements of POC and PON at this station are shown in Table 1 along with the corresponding ATP data from the same hydrocast. Living carbon estimated from ATP (biomass-C = ATP × 250; Holm-Hansen and Booth, 1966) was shown to be less than 30% of the total POC in this depth interval. A separate hydrocast, performed later in the cruise, produced the same result (data not shown).

The vertical distribution of ATP is given in Figure 3. The ATP values measured in the photic zone at this station (18–60 ng ATP l^{-1}) are typical of previous measurements made in this depth interval around the Hawaiian Islands (Bienfang and Szyper, 1981; Karl, Winn, and Wong, 1981b) and are consistent with concentrations for oligotrophic oceans in general (reviewed by

Table 1
Biomass parameters in the photic zone

Depth (m)	POC ($\mu g\ C\ l^{-1}$)	PON ($\mu g\ C\ l^{-1}$)	C:N (wt:wt)	ATP[a] ($ng\ l^{-1}$)	Biomass-C[b] ($\mu g\ C\ l^{-1}$)	Biomass-C as % of total POC
5	39.9	9.5	4.2	18.6	4.7	11.8
50	30.8	4.4	7.1	37.5	9.4	30.5
75	75.4	7.0	11.1	26.8	6.7	8.9
100	35.7	5.8	6.3	33.0	8.3	23.2
110	32.4	5.7	5.6	29.9	7.5	23.1
120	32.0	4.8	6.7	30.1	7.5	23.4
150	21.8	3.2	6.7	12.4	3.1	14.2

[a] Mean of duplicate determinations.
[b] Biomass-C estimated as ATP × 250.

Karl, 1980). The concentration of ATP from 750 to 3,000 m was relatively uniform with depth at about 1–2 ng ATP l^{-1}.

A study was conducted to monitor total ATP concentration in the photic zone over a 24-h period. No consistent change in ATP concentration with time of day was observed (Figure 4). In contrast to the relatively constant concentrations of ATP measured over a 24-h period in the water column, the ATP concentrations in incubation bottles displayed systematic variations during incubation. Table 2 summarizes the changes in ATP concentrations, as a percentage of the initial concentration, during the in situ incubations from 10 to 150 m. Analysis of variance showed that there was a 94% probability that the ATP concentrations measured before and after incubation were different. We also observed that the percentage change decreased from a maximum of 116% at 10 m and became negative for samples below 100 m (Table 2). There was a significant inverse linear relationship ($p > 0.99$) between the percentage change in ATP and depth ($r = -0.92$).

Rates of Nucleic Acid Synthesis and Time Course of Labeling

The results of ^{3}H-adenine time course experiment for an on-deck incubation are shown in Figure 5. The time course of RNA and DNA synthesis showed the effects of compartmentalization of

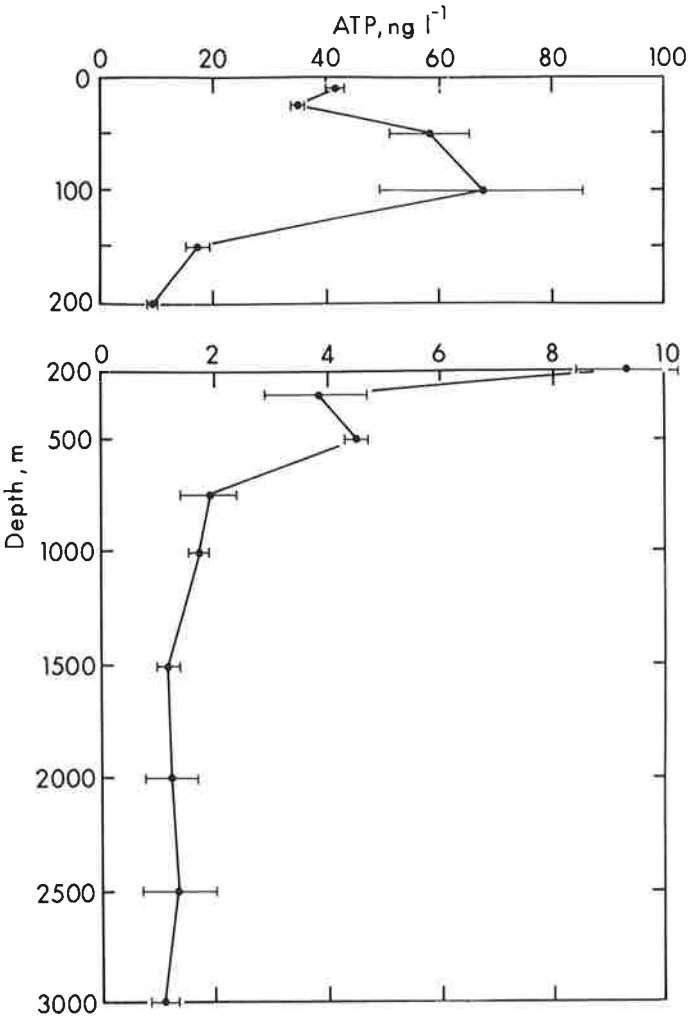


FIGURE 3. ATP concentration as a function of depth. Data shown represent the mean of triplicate measurements, ± one standard deviation unit.

the ATP precursor pool as discussed in Karl, Winn, and Wong (1981a).

A separate calculation of the rate of RNA and DNA synthesis using the total label accumulated in RNA and DNA and the integral of the ATP-specific activity over the length of the time course experiment (Emerson and Humphreys, 1971; Yamazaki

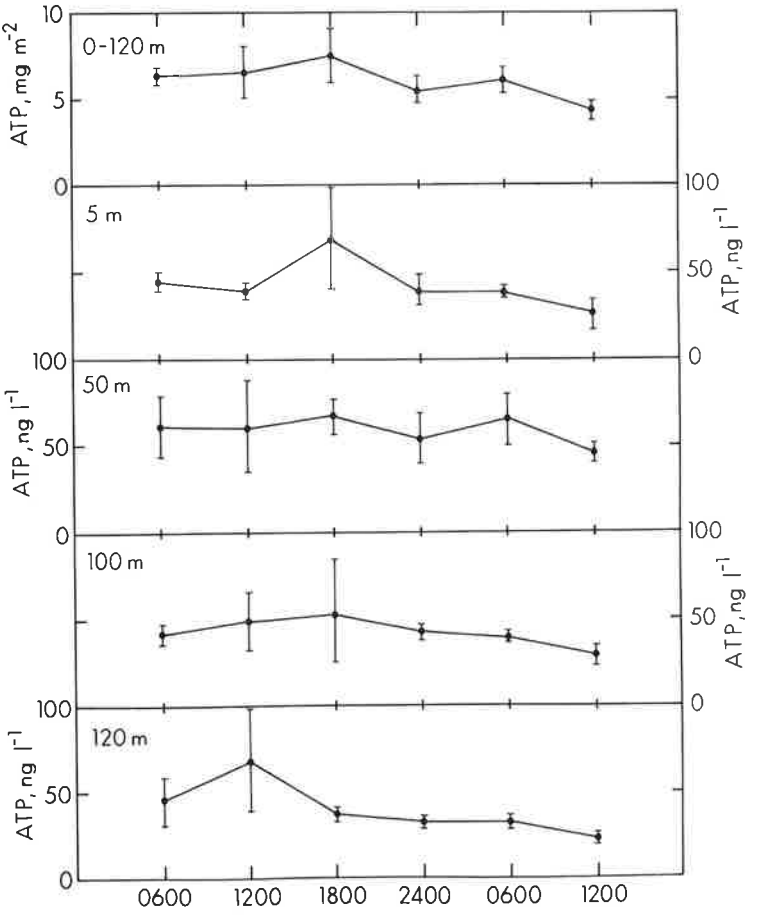


FIGURE 4. ATP concentrations measured in the water column during a 24-h period at four depths in the photic zone and integrated from 0 to 120 m. Data shown represent the mean of triplicate measurements, ± one standard deviation unit. Units on *x*-axis represent local time of day.

and Leung, 1981) was also performed. This calculation yields a total rate of synthesis of 3.6 pmol DNA l^{-1} h^{-1} and 60 pmol RNA l^{-1} h^{-1}. These rates are similar to the rates calculated at discrete points during the time course (Figure 5, bottom). We therefore have confidence that our DNA synthesis rates measured from end point data from 5- and 6.5-h in situ incubations yield accurate nucleic acid synthesis rates.

Table 2
Change in ATP concentrations in incubation bottles[a]

Depth (m)	Initial (ng ATP l^{-1})	Final[b] (ng ATP l^{-1})	Percentage change
10	21.2	45.8	116
25	30.1	44.2	47
50	33.0	53.5	62
75	33.7	49.4	47
100	41.7	39.4	−6
125	20.0	11.9	−41
150	23.4	17.3	−26

[a] All values are the means of duplicate determinations.
[b] "Final" values are those measured in the incubation bottles at the end of a 5-h in situ incubation.

In Situ Rate of RNA and DNA Synthesis

The results obtained from two separate in situ incubations (0–150 m and 250–900 m) are summarized in Figure 6. The total rates of both RNA and DNA synthesis decreased with increasing depth, as might be expected because of the corresponding decline in living biomass (see ATP profile, Figure 3). In contrast, the biomass-specific rates (i.e., rates per unit ATP) of RNA and DNA synthesis increased with increasing depth, implying faster biomass-specific growth rates for the intermediate-depth microbial populations.

Using rates of DNA synthesis (Figure 6), an extrapolation was made to total water column production. Assuming that dAMP represents 25 mole percent of DNA, that DNA represents 2% of cellular carbon by weight (Holm-Hansen, 1969), and that the rate of DNA synthesis does not vary diurnally, the total organic carbon production integrated from 0 to 150 m and from 150 to 900 m was approximately 400 and 790 mg C m^{-2} day^{-1}, respectively.

The growth rates of the microbial populations were also estimated from the data derived from the in situ incubations. The results are summarized in Table 3. The growth rates of the microbial populations in the photic zone ranged from 0.4 to 0.5 doublings day^{-1} whereas the growth rates estimated below 150

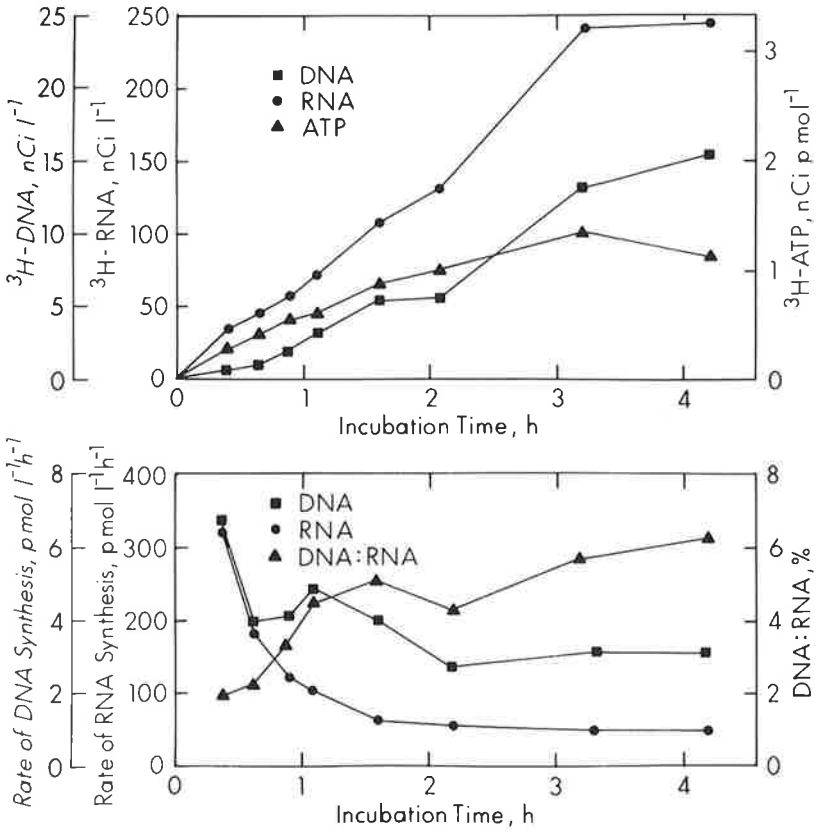


FIGURE 5. Upper frame shows the time course of nucleic acid labeling. Lower frame shows the total rates of RNA and DNA synthesis and DNA:RNA ratio at various times during incubation. The DNA:RNA rate ratio is expressed as ^{3}H incorporated into DNA as a percent of ^{3}H incorporated into RNA. The water sample was collected at 10 m and incubated on deck. Zero hour was 1100 local time.

m ranged from 1.1 to 2.4 doublings day^{-1}. The growth rate at 150 m was intermediate between these values at 0.62 doublings day^{-1}.

Discussion

The POC and PON concentrations and C:N ratios for the photic zone at this station conform to values reported by Sharp et al.

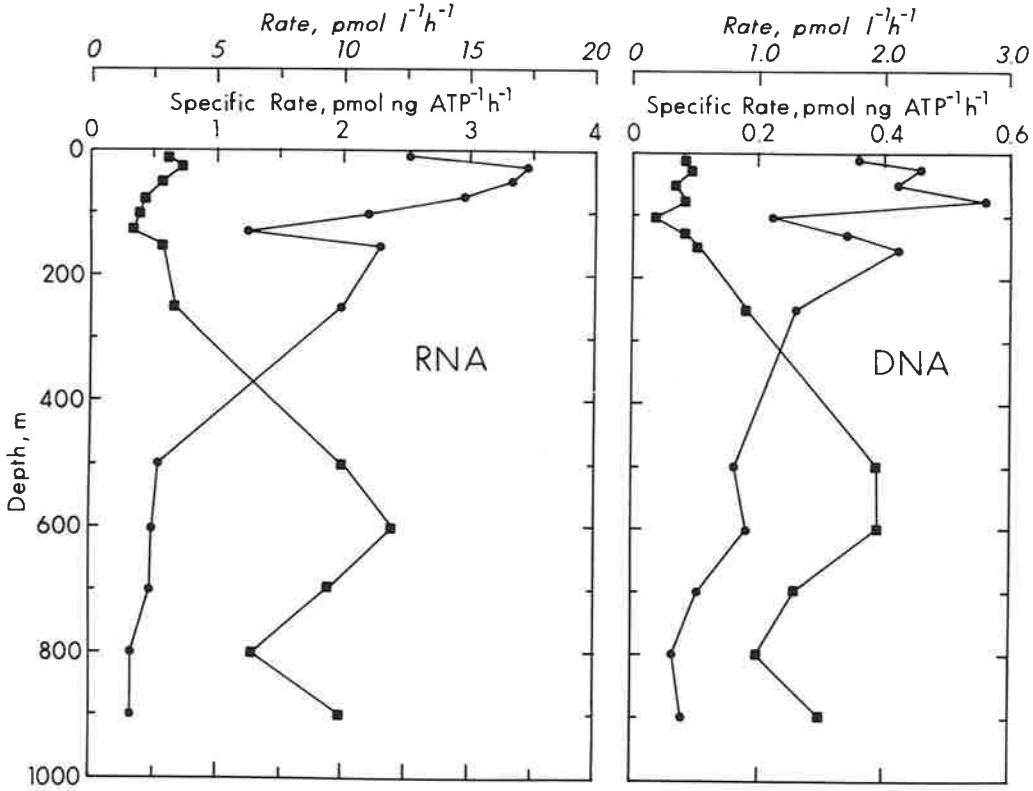


FIGURE 6. Total and biomass-specific rates of RNA and DNA synthesis for in situ incubations from 100 to 900 m. Rates were calculated from end point measurements.

Table 3
Microbial community growth rates

Depth (m)	ATP ($ng\,l^{-1}$)	Biomass-C[a] ($ng\,l^{-1}$)	DNA Synthesis ($pmol\,l^{-1}\,h^{-1}$)	Microbial-C Production[b] ($ng\,l^{-1}\,h^{-1}$)	Growth Rate[c] (doublings day^{-1})
10	24.1	6,030	1.8	110	0.44
25	30.1	7,530	2.3	140	0.44
50	33.6	8,400	2.1	130	0.48
75	33.7	8,420	2.8	170	0.48
125	20.1	5,020	1.7	100	0.48
150	20.2	5,050	2.1	130	0.62
250	7.20	1,800	1.3	80	1.1
500	2.05	513	0.8	50	2.4
600	2.40	600	0.9	55	2.2
700	1.95	423	0.5	31	1.7
800	1.50	375	0.3	19	1.2
900	1.35	338	0.4	25	1.7

[a] Biomass-C estimated from ATP (ATP × 250).
[b] Carbon production estimated from DNA synthesis assuming DNA represents 2% POC by weight.
[c] Doublings day^{-1} calculated as daily carbon production ÷ initial biomass carbon.

(1980) for stations in the central North Pacific Ocean, but the concentrations are higher than those measured at station Gollum in Hawaiian waters (Gordon, 1971). Gordon used Selas Flotronic^{R} filters, which have a greater porosity than the glass fiber filters used in this study and by Sharp et al. (1980). Our estimates of living carbon suggest that between 10 and 30% of the POC in the photic zone is living carbon. Sharp et al. (1980) estimated that phytoplankton carbon (from measurements of phytoplankton cell volume and number) averaged 36% of the total POC in the mixed layer at their central North Pacific stations. Since phytoplankton might be expected to represent a major fraction of the total living carbon in the photic zone, these results appear to be in reasonable agreement. Eppley et al. (1977) have noted that in the photic zone of the neritic waters off southern California, living carbon extrapolated from ATP measurements represented, on the average, slightly more than 100% of POC. These results may imply that the proportion of total POC represented by living carbon declines from neritic to pelagic environments.

Within the limits of precision of our measurements, we observed no significant change in the standing stock of living biomass (as measured by ATP) in the photic zone over a complete diurnal cycle, assuming that there are no significant diurnal changes in the C:ATP ratio in natural populations of microorganisms. Postma and Rommets (1979) have demonstrated substantial diurnal changes in POC and in the surface waters of the equatorial Atlantic Ocean, which suggests that carbon production and consumption are temporally uncoupled in this environment. Our results indicate that the concentration of living microbial biomass in the photic zone in Hawaiian waters is in approximate steady-state (i.e., $dC/dt = 0$), at least on scales of hours to days, and that there are no diurnal fluctuations in standing stock.

Several independent investigators have noted increases in biomass parameters during bottle incubations of oceanic microbial populations (Sutcliffe, Sheldon, and Prakash, 1970; Sheldon, Prakash, and Sutcliffe, 1973; Sheldon and Sutcliffe, 1978; Fuhrman and Azam, 1980; Falkowski and Owens, 1982). Sheldon and Sutcliffe (1978) reported increases in ATP concentrations in incubation bottles in the Sargasso Sea, which they interpreted as microbial production. On occasion, their data extrapolated to doubling times of 3 h for the total microbial community in these oligotrophic waters. In contrast to the relatively constant concentrations of particulate ATP in the water column in our experiments, significant changes in ATP concentrations ($+116\%$ to -41%) did occur during 5-h in situ incubations of surface water. These results indicate that prescreening and/or containment of water samples in incubation bottles disrupts the predator-prey relationships which presumably maintain constant living biomass in the water column. The percentage change in ATP concentration during bottle incubations decreased from a maximum of $+116\%$ at 10 m to negative values (i.e., loss of total ATP during the incubation period) with depths below 100 m. These data are not easily interpreted, since the effects of prescreening and containment of water samples in incubation bottles are largely unknown.

Our DNA synthesis rate measurements suggest a growth rate

for the entire microbial population in the photic zone of approximately 0.4 to 0.5 doublings day^{-1}. These growth rates are within the range of previously published estimates of growth rates of pelagic phytoplankton (Goldman, McCarthy, and Peavey, 1979) and agree with estimates of phytoplankton growth rates in coastal Hawaiian waters (Redalje and Laws, 1981). These growth rate estimates are greater than the 0.2 doublings day^{-1} reported for the phytoplankton of the North Pacific Ocean using $^{14}CO_2$ and $^{32}PO_4$ incorporation data (Eppley et al., 1973; Sharp et al., 1980; Perry and Eppley, 1981), although the factor of 2 might easily be accounted for by differences in the method used to estimate microbial standing stocks. It is important to emphasize, however, that our measurements include the metabolism of both autotrophic and heterotrophic microbial populations and consequently are not directly comparable to previous growth rate estimates.

In situ incubations indicate that the biomass-specific growth rates of the populations below 150 m (1.1 to 2.4 doublings day^{-1}) are greater than those in the photic zone. At present we interpret these results as being due to a shift in the makeup of the microbial community with depth. In the photic zone the measured rates of nucleic acid synthesis are the result of the metabolism of both bacteria and phytoplankton, whereas below the photic zone nucleic acid metabolism is predominantly due to heterotrophic bacteria. Since bacteria have an inherently faster growth rate than phytoplankton, the increased specific rate of synthesis in waters dominated by bacteria is not totally unexpected. Our growth rate estimates are considerably greater than the 0.4 doublings day^{-1} previously reported for bacteria isolated from these depth intervals in the central North Pacific Ocean (Carlucci and Williams, 1978). However, their study involved only a single bacterial isolate from this depth interval and is not directly comparable to the measurements reported here. Considering the current paucity of information regarding the in situ metabolic status of bacteria in the ocean, we feel that these data provide novel information regarding the growth of microbial assemblages in the ocean. The rapid biomass-specific growth rates observed in the intermediate-depth waters may also indicate the presence of

a zone of intense decomposition of sinking organic material from the overlying surface waters. Similar zones of rapid bacterial activity, presumably resulting from the remineralization of sinking organic material, have also been identified in the Caribbean Sea (Karl, 1979) and in neritic waters off central California (Karl and Knauer, in press).

Rates of primary production in Hawaiian waters using $^{14}CO_2$ incubations generally measure less than 100 mg C m^{-2} day^{-1} (Koblentz-Mishke, Volkovinsky, and Kabanova, 1970; Bienfang and Gundersen, 1977; Bienfang and Szyper, 1981). In this study rates of total microbial production estimated from DNA synthesis measurements and integrated from 0 to 150 m are on the order of 400 mg C m^{-2} day^{-1}. Again, we interpret this as the rate of carbon produced by both autotrophic and heterotrophic processes (i.e., the sum of microbial carbon produced from inorganic carbon and from recycled organic carbon). These data suggest that the $^{14}CO_2$ productivity technique may underestimate total microbial community production in these waters, although until the two techniques are compared simultaneously, a discussion of these apparent disparities may not be fully justified. A number of recent studies, using a variety of techniques, have also suggested that $^{14}CO_2$ primary production incubations underestimate organic carbon production in oligotrophic oceans (Sutcliffe, Sheldon, and Prakash, 1970; Sorokin, 1971; Sheldon, Prakash, and Sutcliffe, 1973; Gieskes, Kraay, and Baars, 1979; Goldman, McCarthy, and Peavey, 1979; Shulenberger and Reid, 1981; Jenkins, 1982). The reason(s) for these discrepancies is still open to debate (Eppley, 1980; Goldman, 1980; Peterson, 1980; Eppley, 1982; Kerr, 1983) and experimentation.

Total rates of microbial production estimated from DNA synthesis measurements and integrated over the 150–900 m depth interval suggest a rate of microbial production of 790 mg C m^{-2} day^{-1}. This is nearly twice the rate of microbial production estimated for the photic zone. High rates of microbial production below the photic zone have been reported previously for the equatorial Pacific Ocean (Sorokin, 1971) but have generally been discounted because of uncertainties in the methodology employed (Steeman Nielsen, 1972; Skopintsev, 1973; Banse, 1974).

However, Jenkins (1982), using an entirely separate approach, presents additional evidence for high rates of heterotrophic activity below the photic zone. It is noteworthy that this apparent carbon and energy enigma is not unique to our Hawaiian stations but has been documented in the VERTEX program as well, both at a eutrophic and a mesotrophic station (D. Karl and G. Knauer, in preparation).

The high rates of total carbon production estimated at intermediate depths could, in theory, be an artifact of the methods used. If a major proportion of the microorganisms below 150 m are incapable of assimilating ^{3}H-adenine, an artificially low community ATP pool specific radioactivity, and therefore an overestimate of the rate of nucleic acid synthesis, could result. If this were the case, one might expect the specific activity of the ATP precursor to be substantially lower below 150 m than in the overlying waters. A plot of the specific activity versus depth (Figure 7) shows that the more rapid specific rates of nucleic acid synthesis measured below the mixed layer are actually the result of an increase in the rate of ^{3}H-adenine assimilation per unit biomass, rather than any systematic depth-dependent decrease in the precursor specific activity.

One might imagine that a phytoplankton bloom, producing large amounts of sinking detrital material (Packard et al., 1977), could result in high rates of microbial production at intermediate depth relative to the photic zone. However, we have discounted this possibility, since the tropical oligotrophic oceans are known for their temporal stability. We currently hypothesize that this observation is due to a highly efficient recycling of organic material by the resident microbial populations. The assimilation efficiencies of marine heterotrophs may be as high as 60% (Payne, 1970) or even higher (Williams, 1981). These high assimilation efficiencies coupled with the recycling of organic material can, under steady-state conditions, yield microbial production estimates consistent with our field observations. Obviously further work is required before any firm conclusions can be reached.

In conclusion, our results indicate the following about the oligotrophic waters near the Hawaiian Islands: (1) Living carbon

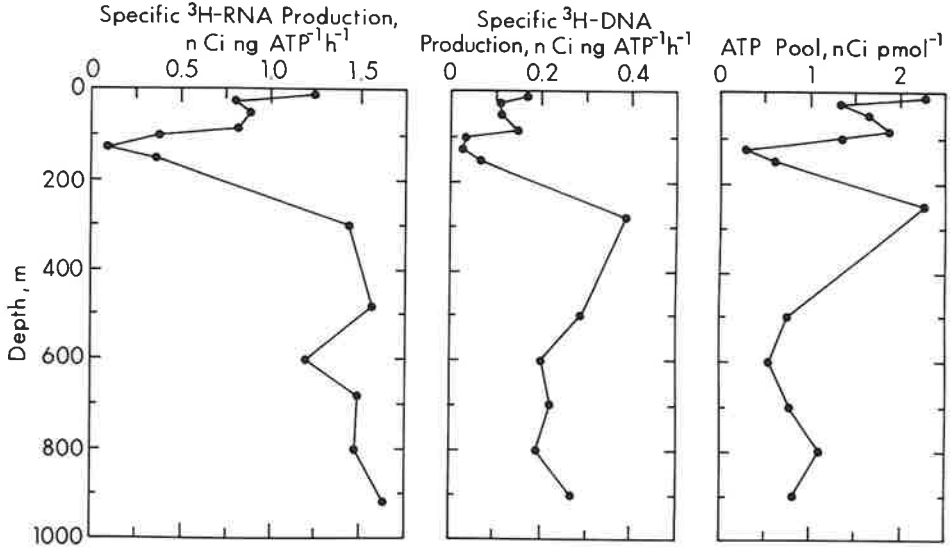


FIGURE 7. Rate of ^{3}H-adenine assimilation into RNA and DNA normalized to biomass (as measured by ATP) and ATP specific activity for in situ incubations from 10 to 900 m.

represents less than 30% of the total particulate organic carbon in the photic zone. (2) The microbial biomass present in the photic zone is in approximate steady-state, at least on the order of days, and there are no large diurnal biomass fluctuations. However, changes in microbial biomass do occur during incubations of prescreened seawater, presumably because of the disruption of predator-prey relationships that maintain constant biomass in the water column. (3) Extrapolations from DNA-synthesis-rate measurements in the photic zone indicate a growth rate for the microbial population as a whole of 0.4 to 0.5 doublings day^{-1} and a total rate of microbial production of 400 mg C m^{-2} day^{-1}. This rate of microbial production is considerably greater than is typically measured in these waters using $^{14}CO_2$ primary production techniques. (4) Extrapolations from DNA synthesis rate measurements in intermediate-depth waters (150 to 900 m) indicate that the specific growth rate of the microorganisms inhabiting this region is higher than the growth rate of the populations inhabiting the overlying waters. Growth rate estimates at intermediate depths ranged from 1.1 to 2.4 doublings day^{-1}. The total depth-integrated microbial production for this depth interval is 790 mg C m^{-2} day^{-1}, almost twice the total microbial production for the 0- to 150-m depth interval. We interpret the increased growth rate to be due to a shift in the makeup of the microbial populations, from one dominated by phytoplankton in the photic zone to one dominated by heterotrophic bacteria in deeper waters, and hypothesize that the high rate of production is due to the rapid and efficient recycling of organic matter derived from the photic zone.

Acknowledgments

The authors wish to express their appreciation to D. Wong, D. Craven, and J. Ditullio for help in obtaining and analyzing the samples, to C. J. Lorenzen and M. J. Perry for their generous donation of ship time and for providing the hydrographic data shown in Figure 2, to K. E. Chave and K. Orrett for their helpful comments on an earlier draft of this manuscript, and to the Captain and crew of the R/V *Thomas Thompson* for logistics support. This work was supported in part by National

Science Foundation grants OCE78–25446 and OCE80–05180 awarded to D. M. Karl.

References

Banse, K., 1974. On the role of bacterioplankton in the tropical ocean. Mar. Biol. 24: 1–5.

Bienfang, P. K, and K. Gundersen, 1977. Light effects on nutrient-limited, oceanic production. Mar. Biol. 43: 187–199.

Bienfang, P. K., and J. P. Szyper, 1981. Phytoplankton dynamics in the subtropical Pacific Ocean off Hawaii. Deep-Sea Res. 28: 981–1000.

Carlucci, A. F., and P. M. Williams, 1978. Simulated in situ growth rates of pelagic marine bacteria. Naturwissenschaften 65:541.

Emerson, C. P., and T. Humphreys, 1971. A simple and sensitive method for quantitative measurement of cellular RNA synthesis. Anal. Biochem. 40: 254–266.

Eppley, R. W., 1980. Estimating phytoplankton growth rates in the central oligotrophic oceans. In: P. G. Falkowski (ed.), Primary Productivity of the Sea. Plenum Press, New York: 231–242.

Eppley, R. W., 1982. The PRPOOS Program: A study of plankton rate processes in oligotrophic oceans. Eos. 63: 522.

Eppley, R. W., E. H. Renger, E. L. Venrick, and M. M. Mullin, 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the Pacific Ocean. Limnol. Oceanogr. 18: 534–551.

Eppley, R. W., W. G. Harrison, S. W. Crisholm, and E. Stewart, 1977. Particulate organic matter in surface waters off Southern California and its relationship to phytoplankton. J. Mar. Res. 35: 671–696.

Falkowski, P. G., and T. G. Owens, 1982. A technique for estimating phytoplankton division rates using a DNA-binding fluorescent dye. Limnol. Oceanogr. 27: 776–782.

Fuhrman, J. A. and F. Azam, 1980. Bacterioplankton secondary production estimates for the coastal waters of British Columbia, Antarctica, and California. Appl. Environ. Microbiol. 39: 1085–1095.

Gieskes, W. W. C., G. W. Kraay, and M. A. Baars, 1979. Current ^{14}C methods for measuring primary production: Gross underestimates in oceanic waters. Neth. J. Sea Res. 13: 58–78.

Goldman, J. C., 1980. Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology. In: P. G. Falkowski (ed.), Primary Productivity of the Sea. Plenum Press, New York: 179–194.

Goldman, J. C., J. J. McCarthy, and D. G. Peavey, 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 279: 210–215.

Gordon, D. C., 1971. Distribution of particulate organic carbon and nitrogen at an oceanic station in the central Pacific. Deep-Sea Res. 18: 1127–1134.

Holm-Hansen, O., 1969. Algae: Amounts of DNA and organic carbon in single

cells. Science 163: 87–88.
Holm-Hansen, O., and C. R. Booth, 1966. The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol. Oceanogr. 11: 510–519.
Jenkins, W. J., 1982. Oxygen utilization rates in North Atlantic subtropical gyre and primary production in oligotrophic systems. Nature 300: 246–248.
Johnson, K. M., C. M. Burney, and J. McN. Sieburth, 1981. Enigmatic marine ecosystem metabolism measured by direct diel CO_2 and O_2 flux in conjunction with DOC release and uptake. Mar. Biol. 65: 49–60.
Karl, D. M., 1979. Measurement of microbial activity and growth in the ocean by rates of stable ribonucleic acid synthesis. Appl. Environ. Microbiol. 38: 850–860.
Karl D. M., 1980. Cellular nucleotide measurements and applications in microbial ecology. Microbiol. Rev. 44: 739–796.
Karl, D. M., 1981. Simultaneous rates of ribonucleic acid and deoxyribonucleic acid synthesis for estimating growth and cell division of aquatic microbial communities. Appl. Environ. Microbiol. 42: 802–810.
Karl, D. M., 1982. Selected nucleic acid precursors in studies of aquatic microbial ecology. Appl. Environ. Microbiol. 44: 891–902.
Karl, D. M., and O. Holm-Hansen, 1978. Methodology and measurement of adenylate energy charge ratios in environmental samples. Mar. Biol. 48: 185–197.
Karl, D. M., and G. A. Knauer, in press. Vertical distribution, transport, and exchange of organic matter in the northeast Pacific Ocean: Evidence for multiple zones of biological activity. Deep-Sea Res.
Karl, D. M., C. D. Winn, and D. L. Wong, 1981a. RNA synthesis as a measure of microbial growth in aquatic environments: Evaluation, verification, and optimization of methods. Mar. Biol. 64: 1–12.
Karl, D. M., C. D. Winn, and D. L. Wong, 1981b. RNA synthesis as a measure of microbial growth in aquatic environments. II. Field applications. Mar. Biol. 64: 13–21.
Kerr, R. A., 1983. Are the oceans' deserts blooming? Science 220: 397–398.
Koblentz-Mishke, O. J., V. V. Volkovinsky, and J. G. Kabanova, 1970. Plankton primary production of the world ocean. In: W. S. Wooster (ed.), Scientific Exploration of the South Pacific. National Academy of Science, Washington, D.C.: 183–193.
Packard, T. T., H. J. Minas, T. Owens, and A. Devol, 1977. Deep-sea metabolism in the eastern tropical North Pacific. In: N. R. Anderson and B. J. Zahuranec (eds.), Oceanic Sound Scattering Prediction. Plenum Press, New York: 101–116.
Payne, W. J., 1970. Energy yields and growth of heterotrophs. Annu. Rev. Microbiol. 24: 17–52.
Perry, M. J., and R. W. Eppley, 1981. Phosphate uptake by phytoplankton in the central North Pacific Ocean. Deep-Sea Res. 28: 39–49.
Peterson, B. J., 1980. Aquatic primary productivity and the $^{14}CO_2$ method: A history of the productivity problem. Annu. Rev. Ecol. Syst. 11: 359–385.

Pomeroy, L. R., 1974. The ocean's food web, a changing paradigm. BioScience 24: 499–504.

Postma, H., and J. W. Rommets, 1979. Dissolved and particulate organic carbon in the North Equatorial Current of the Atlantic Ocean. Neth. J. Sea Res. 13: 85–98.

Redalje, D. G., and E. A. Laws, 1981. A new method for estimating phytoplankton growth rates and carbon biomass. Mar. Biol. 62: 73–79.

Ryther, J. H., 1969. Photosynthesis and fish production in the sea. Science 166: 72–76.

Sharp, J. H., 1974. Improved analysis for "particulate" organic carbon and nitrogen from seawater. Limnol. Oceanogr. 19: 984–989.

Sharp, J. H., M. J. Perry, E. H. Renger, and R. W. Eppley, 1980. Phytoplankton rate processes in the oligotrophic waters of the central North Pacific Ocean. J. Plankton Res. 2: 335–353.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe, 1973. The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. Limnol. Oceanogr. 18: 719–733.

Sheldon, R. W., and W. H. Sutcliffe, Jr., 1978. Generation times of 3 h for Sargasso Sea microplankton determined by ATP analysis. Limnol. Oceanogr. 23: 1051–1055.

Shulenberger, E., and J. L. Reid, 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered. Deep-Sea Res. 28: 901–919.

Sieburth, J. McN., 1976. Bacterial substrates and productivity in marine ecosystems. Annu. Rev. Ecol. Syst. 7: 259–285.

Sieburth, J. McN., K. M. Johnson, C. M. Burney, and D. M. Lovoie, 1977. Estimation of in situ rates of heterotrophy using diurnal changes in dissolved organic matter and growth rates of picoplankton in diffusion chambers. Helgol. Wiss. Meeresunters. 30: 565–574.

Skopintsev, B. A., 1973. A discussion of some views on the origin, distribution, and composition of organic matter in deep ocean waters. Oceanology 12: 471–474.

Sorokin, J. I., 1971. On the role of bacteria in the productivity of tropical oceanic waters. Int. Rev. Gesamten Hydrobiol. 56: 1–48.

Steeman Nielsen, E., 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. J. Cons. Int. Explor. Mer 18: 117–140.

Steeman Nielsen, D., 1972. The rate of primary production and the size of the standing stock of zooplankton in the oceans. Int. Rev. Gesamten Hydrobiol. 54: 513–516.

Sutcliffe, W. H., Jr., R. W. Sheldon, and A. Prakash, 1970. Certain aspects of production and standing stock of particulate matter in the surface waters of the Northwest Atlantic Ocean. J. Fish. Res. Board Can. 27: 1917–1926.

Tijssen, S. B., 1979. Diurnal oxygen rhythm and primary production in the mixed layer of the Atlantic Ocean at 20°N. Neth. J. Sea Res. 13: 79–84.

Williams, P. J. leB., 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. Kiel. Meeresforsch. 5: 1–28.

Yamazaki, H., and K. Leung, 1981. Determination of the total rate of synthesis and degradation of RNA in bacterial cultures. Can. J. Microbiol. 27: 168–174.